THE PEANUT

(*Arachis hypogea*)

ITS HISTORY, HISTOLOGY, PHYSIOLOGY, AND UTILITY

BY

RALPH AUGUSTUS WALDRON, B.S., M.S.

Thesis Presented to the Faculty of the Graduate School of the University of Pennsylvania, May 1918, in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

PHILADELPHIA, PA.
1918

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With Plates LXXIX and LXXX

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Introduction

Few plants present as great interest or diversity of problems for botanical study as the peanut. Agriculturally it is of great importance as a soil renovator and forage plant. From an economic standpoint, its products are of great value, every part of the plant being of some direct or indirect use. The peanut, potato, cotton, tobacco and Indian corn,—five plants which are exerting great influence in the world's commerce and industries—were contributed by the new world. The peanut, although still in the background of some of these, promises to rival, if not surpass, them in importance. It is often grown in the economic house of botanical gardens and as a novelty out of doors. After a brief botanical study of the plant from the morphological standpoint, certain problems were presented which bear an important relation to its physiology, and are rather striking in their bearing on some well known ecological problems. A study of the history of the plant, and brief discussions concerning its economy in nature and its utilization by man, have now been taken up in succeeding pages. The writer, in here recording these observations, feels that he has made but a beginning and hopes to continue investigations in the future.

The writer wishes to express his grateful appreciation to Professor John M. Macfarlane, of the University of Pennsylvania, for his many suggestions and kind guidance in working up this treatise.

History

Introduction. With few exceptions, authors agree that the original home of the peanut (*Arachis hypogaea*) is uncertain. In the mind of the writer, there are sufficient facts at hand to state definitely, as have one or two already, that it is a native of Brazil, although, as with many other extensively cultivated plants, it has never been recognized in the truly wild state. There is no evidence to contradict the view that it is a native of this part of South America. The writer gives below a synopsis of his studies regarding the native home of the plant and its history so far as known in relation to man.

Early American Records. The earliest mentions in any existing literature are those pertaining to Brazil and Peru, and these antedate any found in European works. Acosta[1], in his work published in 1598, refers to it along with other plants which are native to Brazil, and calls it "mani," a name still applied to it among Spanish

speaking people of South America. Monardes[2], according to Marcgraf and Piso[3], indicated its presence in Peru about this time, giving it the name of "anchic." Aside from these and other early mentions in literature, fruits of the plant were found in tombs at Ancon, Peru. Their presence there undoubtedly antedates the Spanish conquest, and so, also, any written record. According to Dubard[4], it was taken from Brazil to Peru sometime before the

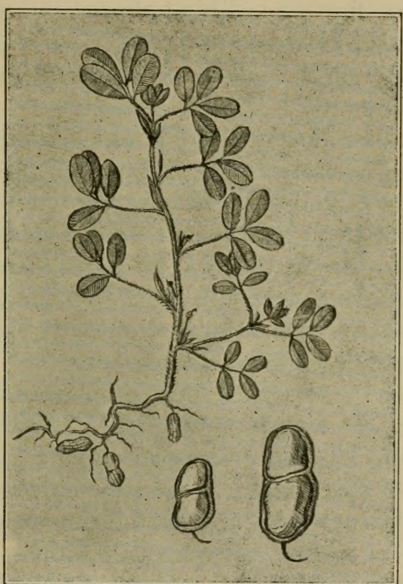

Figure 1 (after Marcgraf & Piso). Mundubi Braziliensis.

sixteenth century and there "was cultivated from an early unknown date." Among European works, Parkinson[5] in his celebrated "Theatrum Botanicum" published in 1640, gives an illustration of the fruit, which is very likely the first. A few years later, (1648) Marcgraf and Piso were the first to figure the whole plant (Fig. 1). It seems worth while to quote parts of Parkinson's quaint description as follows:

"ARACHUS υπογεια AMERICANUS. UNDERGROUND CICHELING OF AMERICA OR INDIAN EARTHNUTS."

"The Indian Earth-nuts (the figure whereof, I give you together as they are termed to us by them that have brought them us) are

very likely to grow from such like plants as are formerly described, (Species of *Vicia*) not onely by the name but by the sight and taste of the thing it selfe, for wee have not yet seene the face thereof above ground, yet the fruit, or Pease-cods (as I may so call it) is farre larger, whose outer huske is thicke and somewhat long, round at both ends, or a little hooked at the lower end, of a sullen whitish color on the outside, striped, and as it were wrinkled, bunching out into two parts, where the two nuts (for they are bigger than any Filberd kernell) or Pease doe lie joyning close one unto another, being somewhat long, with the roundnesse firme and solide, and of a darke reddish colour on the out side, and white within tasting sweet like a Nut, but more oily."

Concerning the introduction into Europe Parkinson's discussion indicates that they were introduced into Portugal. He received specimens sent from Candy and Lisbon. To quote him further he states that the Indian earthnuts are found in "most places of America, as well as to the South, as West parts thereof, both on the Maine and Islands; and generally called by our English Sea-men that goe into those parts Earth-nuts, erroneously enough, as they do most other things that they there meete with."

Eight years after Parkinson's reference the plant was described as follows by Marcgraf and Piso—"Mundubi Brasiliensis Herba, in pedalem aut bipedalem altitudinem adsurgit, caule quadrato aut striato, ex viridi ruffescente & piloso. Hinc inde enascuntur ramuli primo quasi caulem amplectentes & foliolis angustis, acuminatis stipati; mox habent nodum ac trium vel quatuor digitorum longitudine extenduntur; continetq; quilibet ramulus quatuor folia, duo semper sibi opposita paulo plus quam duos digitos longa sesquidigitum lata superne, laete viridia, instar trifolii, inferne paulum canescentia, nervo conspicuo & subtilibus venulis quasi parallelis dotata, raris quoque pilis vestita. Ad exortum ramulorum qui folia gerunt prodit pediculus sesquidigitum circiter longus, tenuis, flosculum gerens flavum & per oras rubentem duobus foliolis constantem, more viciorum aut trifolii. Radix illius haud longa, tenuis, contorta, filamentosa, cui adnascuntur folliculi ex albicante grysei, figura minimae cucurbitae, oblongae, magnitudinae Myrobalani fragiles: quilibet autem continet in se duos nucleos, pellicula saturate purpurea vestitos, carne intus alba, oleaginosa, sapore pistaceorum, qui comeduntur cocti & inter bellaria aponuntur. Multum tamen comesti capitis dolores causare ajunt. Fructu integro quassato nucle intus strepunt"

Linnaeus[6] says it inhabits Surinam, Brazil and Peru, but does not state whether it is wild or cultivated.

Lack of Evidence as to its extra-American Origin. Among old world literature antedating the 16th century, no mention is made. It was thus unknown there before the discovery of the new world. According to Watt[7], all Greek, Latin, Bengalese and Arabian writers are silent concerning the plant. This is very significant since the peanut is too valuable a plant to have been known to Sanskrit speaking peoples and not be used by them. Such a plant could hardly have an antiquity among them without some record being kept. Until quite recently a mention by Theophrastus of an Egyptian grown plant was thought by some, to be a reference to *Arachis*, but this has since been disproved. If it had ever existed in Egypt it could still be found there. Furthermore no mention is made of it in the works of Forskal[8] or Delile[9]. It is not recorded by any early writer on the flora of India. According to De Candolle[10] in Dr. Bretschneider's study of Chinese works[11], the statement is made that its introduction into that country was in the *sixteenth* century. It is not mentioned in ancient Chinese literature. This suggests the possibility of its introduction there from Peru by such expeditions as Magellan's.

De Candolle states: "The antiquity of its cultivation in Africa is an argument of some force which compensates to a certain degree its antiquity in Brazil." The only points offered to indicate an African antiquity are (1) the statement by Sloane[12] that it was used as food on the early slave ships sailing between Africa and America, and (2) that it now has a wide area of cultivation there, both of which could very readily have occurred after its introduction from Brazil. The writer would suggest that the very earliest ships to sail from Brazil to Africa took seeds of *Arachis* to that place, and the environment of the west coast being ideal for its growth, its cultivation very early became widespread; and this has, during the last century, developed into a great industry in the French colonies.

Pison, in his early Brazilian work figures a somewhat similar plant, in its habit of fruit production, to *Arachis*, but states it to be African, while he says *Arachis* is Brazilian. This was a species of *Voandzeia.* To quote De Candolle again, he states, "the silence of Greek, Latin and Arab authors, and the absence of the species in Egypt at Forskal's time lead me to think that its cultivation in Guinea, Senegal, and the east coast of Africa is not of very ancient date; neither has

it the marks of a great antiquity in Asia. No Sanskrit name for it is known, but only a Hindustani one. Rumphius[13] says that it was imported from Japan to several islands of the Indian Archipelago. It would in that case have borne only foreign names, like the Chinese name, for instance, which signified "earth bean." At the end of the last century (19th) it was generally cultivated in China and Cochin-China. Yet, in spite of Rumphius's theory of an introduction into the islands from China or Japan, I see that Thunberg does not speak of it in his Japanese Flora. Now, Japan has had dealings with China for sixteen centuries, and cultivated plants, natives of one of the two countries, were commonly early introduced into the other. It is not mentioned by Forster among the plants employed in the small islands of the Pacific. All these facts point to an American origin." No authors speak of it wild or uncultivated in either hemisphere. Those who speak of it in Asia or Africa carefully say it is cultivated. Piso, in writing of Brazil, says the species is planted. Marcgraf does not mention it as cultivated, indicating however that it may have been. As to foreign names such as the Chinese, meaning "earth-bean," they are all such as would occur to any one upon seeing the plant. Contrary, therefore, to the suggestion of some authors, little significance need be attached to the American names not having accompanied it in its travels to Japan and the Orient.

According to Watt, Sir George Birdwood in his Bombay products gave it a Sanskrit name meaning earth-gram. This name has been repeated by some subsequent writers without the authenticity of it being inquired into.

Distribution. According to Bentham[14] in "Flora Brasiliensis," there are seven species of *Arachis* found in Brazil, six of which are found in the wild state. The other (*A. hypogaea*) he states is generally cultivated in all warm parts of the world. Now, De Candolle well remarks in this relation that: "A genus of which all the well known species are thus placed in a single region of America can scarcely have a species common to both hemispheres; it would be too great an exception to the law of geographical botany." By referring to the accompanying outline map (Figure 2) which shows the reported distribution of these species it will be noted that *A. prostrata* is the most widespread, and *A. pusilla* the most restricted of the group.

The writer asks if varieties of this plant, so generally grown in such environment as exists in Brazil, may not be cultivated forms of one or more Brazilian species?

Of the several cultivated varieties grown today there are recognized two general types of plants as follows: (1) The bunch type, growing erect and bearing its fruit around the base of a single stem. The Spanish variety is an example. It can withstand considerable moisture conditions and its erectness suggests a shade loving tendency. (2) The trailing type, with its several branches spread on the soil, succeeds best in a hot sandy soil, indicating greater xerophytic tendencies. The Jumbo variety is an example. Now, the wild Brazilian species *A. pusilla*, is an erect plant, simulating the

Figure 2
Outline Map of Brazil indicating the reported distribution of the different species of *Arachis*.

1. *A. pusilla.*
2. *A. prostrata.*
3. *A. villosa.*
4. *A. glabrata.*
5. *A. marginata.*
6. *A. tuberosa.*

bunch variety and is reported as growing in dry woods and shady places. Another, *A. prostrata*, is more trailing and grows in open sandy places and so, simulating the prostrate cultivated variety, is

more xerophytic. *Thus the possibility is suggested, first, that the cultivated bunch varieties are derived from such a species as A. pusilla and second, that the prostrate varieties are derived from A. prostrata.* Other evidence in support of this theory is seen in the marked difference in the histology of the fruits of the two domesticated varieties.

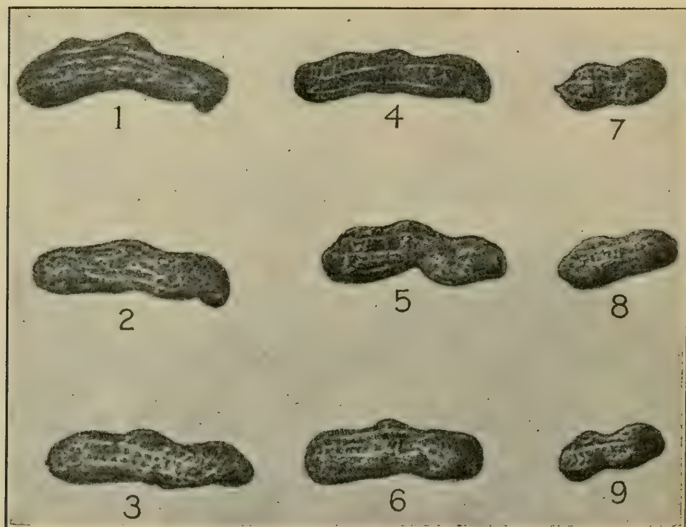

Figure 3 (after Dubard)
Types of peanuts taken at random from
1. Tombs at Ancon, Peru.
2. Java.
3. Tonkin.
4. Madagascar.
5. Madagascar.
6. Spain.
7. Dahomey.
8. Senegal.
9. Spain.

The following summary taken from Dubard further indicates the possibility of our present day varieties being derived from two such wild plants. He states that there were two types of peanuts distributed over the world from South America; one being a two-seeded Brazilian type and the other a three-seeded Peruvian type. The first form was carried to West Africa by Portuguese negroes,

according to this author. It was taken to Europe by early travelers, the Portuguese being there the first propagators, as indicated by Parkinson and others. Further evidence in support of this eastward distribution, which seems more natural from the geographical standpoint, is, that (1) all early illustrations of European and Brazilian works show two seeds, and (2) those of West Africa are two-seeded. The Peruvian type was a variety created in Peru from a form carried there from Brazil some time before the sixteenth century. The question now arises as to the possibility of this plant being a different species from the common two-seeded type. Bentham states the number of seeds to vary from one to three in this genus. This being true, any species might well have been selected. However, Dubard later describes differences in the structure of these which are sufficiently marked to separate them into species. About Magellan's time, this three-seeded form was carried from Peru, to the Moluccas, Phillipines, Indo-China, Asia and Madagascar. If this is true, we should find the three-seeded fruits in these Pacific localities, and this Dubard proves to be true, by comparing specimens taken at hazard from Java, Indo-China and Madagascar. (Figure 3.)

Finally, if peanuts of to-day from Spain and North America be examined, the above two types will be found, indicating a meeting again of these, after having been carried around the world in opposite directions, yet remaining distinct in character. The Peruvian form was undoubtedly carried north and east, but at a date much later than its westward spread. The supposition, according to record, that the two were present at about the same time,—the one in Africa and Europe, the other in the Orient,—further supports this view. Watt states that one name given it in India, where it is much cultivated, is "Manilla-Kottai." This suggests its introduction there from the Phillipines. All these facts relating to the distribution are suggestive, when the lack of evidence of its presence during ancient times in China, India, Africa and Europe is considered.

Since Dubard does not describe the plants of his two forms, it is impossible to determine whether or not they might correspond to the erect and prostrate types. He does describe the fruit and seed of each, however, and it is found that his Brazilian form corresponds to some of the erect, and his Peruvian form to some of the prostrate varieties of to-day. If such a history is possible, which does not seem unlikely, the reported distribution of the two wild species—*A. prostrata* and *A. pusilla*—is again significant. The former,

found in all parts of Brazil, would be the one most naturally carried to Peru rather than the more restricted latter species that is found only in the eastern part. The lack of full descriptive literature on the distribution and morphology of wild and cultivated varieties opens up opportunities for further investigation.

To-day, varieties are rapidly being increased in number by man. This fact, with the ease of intercourse between different countries, explains in part at least why there are such varieties as the Virginian, Spanish, African, Asiatic, etc. It does not indicate in any way the native home of the peanut, which is undoubtedly Brazil.

Recent Literature. During the last 25 years most of the literature on the peanut has been largely concerned with either its culture, uses or chemistry. The writer does not attempt to summarize these and includes titles of but a few of the more recent publications in his bibliography. By referring to the Experiment Station Record of the United States Department of Agriculture, many such references may be found. During the past few years, publications concerning its culture and varieties have been issued by several of the Agricultural Experiment Stations of those southern states in which the peanut is becoming an important crop.

Concerning the study of the plant from a morphological standpoint, little has been done. In 1895, Pettit[15] worked on the fruit stalk. She described its structure in detail and discussed its physiological relation to the plant.

Winton[16] published the results of a histological study of the mature fruit, undertaken especially to secure data for use in the microscopical examination of peanut products. In this relation he described and illustrated the cell structure of the fruit, testa and cotyledons. Adam[17] in 1908 published a fine work concerning its history, growth habits, varieties, culture, products and industry in western Africa.

General Morphology

Description. Since there are two well recognized forms of the peanut plant, the author suggests a division of the Linnaean species into the two sub-species—(1) *fastigiata* for the bunch type, and (2) *procumbens* for the prostrate type, and including under each a number of varieties. Adam gives the full species name *asiatica* for the former, and *africana* for the latter. Such are not only names of varieties and localities, but suggest an erroneous origin. The fol-

lowing is a description of the species, the suggested sub-species and the common varieties.

Arachis hypogaea

Family Leguminosae *Sub-family Hedysareae*

An herbaceous annual.

Roots—fibrous, delicate and white when young. Root hairs usually in rosettes at the base of the side roots—rarely with normal tip hairs. Nodules spherical; surface gray, interior pink; appearing when plants are 8–10 weeks old.

Hypocotyl—2–8 cm. long, sometimes slightly swollen at base during germination.

Stems—30–80 cm. long, erect, or prostrate, more or less hairy, tough, flexible, slightly quandrangular. Main stem usually branching early into cotyledonary branches.

Cotyledons—low epigeal, green, with short, thick petiole; remaining fleshy for two to three weeks, when they dry and drop off.

Leaves—sensitive to light, 8–12 cm. long, alternate, stipulate, pinnately compound. *Stipules* linear-lanceolate, erect, striate. *Petiole* straight, firm, with a single groove along the upper side; a pulvinus at its base. *Leaflets* 2–5 cm. long, four in two pairs, oblong to obovate; apex rotund and tipped by a tiny spine; veins pinnately arranged; under surface slightly hairy; each attached to the petiole by a short pulvinus which causes them to close together vertically in pairs at night.

Inflorescence—an axillary, usually three flowered, fascicled and reduced head.

Flowers—yellow, the larger more terminal ones usually sterile and adorning the plant for some time; the more axial numerous, basal ones usually fertile, smaller, more or less hidden, and born on short peduncles which elongate after fertilization. *Calyx* forming a long stalk-like tube with one narrow lobe as a lower lip, the upper broad and four-toothed. *Corolla* with a large yellow, orange-striped standard, two small wings, and a tiny, incurved, beaked keel. *Stamens* ten, monadelphous, versatile; five often with fertile anthers attached near their base; the alternate ones absent or short and fixed at their center. *Pistil* monocarpous; style long, slender; ovary small, at base of the long calyx tube, one celled with one to six ovules; after fertilization the floral envelopes drop away, and the ovary, now sharp-pointed and strengthened, is pushed by the rigid, recurv-

ing pedicel one to three inches into the soil; after penetration it begins to swell and ripen into a fruit.

Fruit—an indehiscent legume, oblong, reticulated, thick, coriaceous, beaked, swollen around the contained seeds, provided with absorptive hairs when nearing maturity. *Fruit stem* or gynophore reddish and slightly hairy above the soil—white and matted with absorbing hairs below.

Seeds—1–1 ½ cm. long; cotyledons thick, fleshy, oily; radicle short, straight. *Testa* thin, papery, membranous, varying from cream to pink to dark red color.

Sub-species—fastigiata Waldron

Main stem erect and branches all in an upward diagonal position, giving the plant a bushy appearance. Fertile flowers axially grouped near base of plant. Fruit clustered below the main stem. Seeds usually small and oblong.

Variety—White Spanish

Plant 20–30 cm. tall in average soils—foliage abundant and heavy. Pods small, adhering well to the plant, entirely filled by two seeds with pink to brownish testa. Very productive with high oil content.

Variety—Red Spanish

Similar to the White Spanish, except that the seed coats are red and the pods somewhat larger—less productive than the White Spanish.

Variety—Valencia

Plant 25–50 cm. tall. Pods long, medium thickness, clinging poorly to the plant, and containing two to four closely crowded seeds with red testas.

Variety—Tennessee Red

Plants similar to those of the Spanish varieties. Pods long, clinging to the plants and containing two to six seeds with dull red seed coats.

Sub-species—procumbens Waldron

Loosely branching, spreading plants (semi-erect in one variety); the stems often later ascending. Flowers and fruit considerably scattered along the prostrate stems. Seeds large, more or less pointed.

Variety—North Carolina, Florida Runner, African, Wilmington, etc.

Rank growing plants with dark green massive foliage. Pods not clinging well, medium sized, containing two, sometimes three, moderate-sized seeds with reddish testas.

Variety—Virginia Runner

Similar to the North Carolina, but with much larger pods and seeds.

Variety—Virginia Bunch

Plants semi-erect with light foliage, often appearing among plants in fields of the Runner type. Pods large, adhering well to the plant, bright, clean, with two, sometimes three, seeds covered by light brown coats.

Variety—Jumbo

The same as, or possibly sometimes a strain of, the Virginia Runner or Virginia Bunch varieties.

Histology

Root

The internal structure of the root of *Arachis* is of the normal dicotyledonous type. The epidermal relation, however, of young roots and the production of root hairs is quite striking. It has been reported by Pettit and Richter[18] that no hairs are produced on the plant. The author, however, found them on all plants examined but usually in different position from the normally produced tip hairs. Although the tip hairs were found, they were rare and appeared only on young vigorous plants. Usually they are present in the form of rosettes on and at the base of newly formed side roots. As seen in Plate LXXIX, Fig. 4, those produced nearest the base are comparatively long, but are gradually reduced in length until none appear. Aside from the position relation, these rosette hairs are of the normal root-tip hair structure. The tip hairs when present are usually rather short and scattered, occurring on young delicate, usually few-branched, roots. No hairs of either type have been observed on the main root either during germination or later.

Young elongating roots of the plant which bear no root hairs often have their cuticle mucilaginized causing the soil particles to adhere as if hairs are present. These roots are often very white, delicate

and semi-transparent. Placing a portion of one on a slide for examination under the microscope must be done with care, for the epidermal and outer cortex cells seem readily to fall apart like so many poorly cemented bricks becoming loosened. This is due, in part at least, to pressure from within, since, as noted by Pettit, the inner meristems develop much faster than the dermatogen. This is markedly evident on the primary root where the surface cells are continually peeling off in rows or patches. Sufficient protection, according to Pettit, is afforded by a cutinized outer wall being formed by the cells which become exposed. Pettit also states that the lateral roots act in a similar way, but the present writer did not find this to be the case with his plants. These roots are always normal in this regard, although very delicate. As they increase in age, their outer surface is supplied with a regular periderm, and it is only in the early stages of radicle growth that this peculiar habit is observed.

Stem

The stem is normal for dicotyledons. The epidermis is composed of a layer of small, thickly cuticularized cells interrupted by stomata in young stems and by a corky lenticel proliferation in old ones. Three-celled hairs are scattered along young stems. These are typical of many other Leguninosae, each hair having a long pointed terminal cell with two tiny, flattened basal cells. There are also small crystal cells arranged in groups of two to four, each containing one rectangular crystal. The cortex is six to eight layered and composed of much larger thin walled cells. At the outer extremity of the primary bundle areas of the vascular system are large patches of highly indurated hard bast. This, along with the quite extensive and considerably indurated xylem, give a tough and flexible character to the stem. The pith in young stems is composed of round extremely thin walled cells filled with starch. As the stem matures, however, the pith becomes more or less broken down resulting in a semi-hollow condition. Concerning the cambium, a very interesting relation is noted later as to its development in the fruit stalk (see page 314).

Leaf

The leaf structure of the peanut is most striking, especially when the xerophytic tendencies of the plant are considered. There are numerous average-sized stomata on both surfaces that are neither

raised nor sunken. They average from fifteen to twenty per square millimeter, and each is surrounded by two unequal subsidiary cells. Both epidermal layers are also supplied with numerous specially formed crystal cells (Plate LXXIX, Fig. 5.) which, when the leaf is young, are small, each containing a single rounded crystal. Later, these cells become fused into what might be called an "epidermal vessel," irregular in shape and containing two to thirty crystals arranged in clusters or irregular rows. Solereder[19] notes the presence of these, but does not mention the later fusion into one. In attempting to determine the origin of these, a stem apex with a young bud attached was sectioned. It was found that in very young leaves all the epidermal cells were alike, and devoid of crystals. Immediately after the last cell division, however, some of the cells increased in size to form the normal epidermis, while others remained small to become the crystal-containing cells. In some of these it was noted that the small crystal seemed to be a part of the nucleus, possibly formed within and by it. It was in a pellicle-like projection which later separated away. In all such young cells the crystal was imbedded in a protoplasmic matrix which gradually became mucilaginized in old cells. The mesophyll of the leaf is composed of a two- to five-layered palisade tissue immediately below the upper epidermis and a single layer of water storage cells next to the lower. These two features are more typical of a xerophytic plant than is the presence of the above mentioned stomata. A loose, comparatively thin layer of spongy mesophyll separates the palisade and water storage layers. The petiole and lower epidermis of the leaflets bear the typical three celled hairs already mentioned as found on the stem.

Fruit

The anatomy and physiology of the fruit were carefully studied for the purpose of discovering, if possible, some facts concerning its hypogeal development. Among other members of the Leguminosae to share this peculiarity are *Amphicarpa monoica*, *Trifolium subterraneum*, species of *Voandzeia* and of the new African genus *Kerstingiella*. *Amphicarpa* bears two kinds of flowers, and accordingly two forms of fruit, only one of which develops underground. The flower which gives rise to this subterrenean fruit is formed and always remains underground. *Trifolium subterraneum* bears but one type of flower formed in heads. The peduncle, after flowering,

lengthens and sinks into the soil carrying the head with it. The seeds do ripen above ground, however, and will germinate.

Differing from both of these, *Arachis* and the other two genera mentioned above have a nearly uniform type of flower, the ovary of which is pushed into the ground by a growth at its base. The elongating fruit stalk is called a "gynophore."

Anatomy of the Young Gynophore. Observations by the writer correspond to most of those of Pettit, whose article is chiefly concerned with the structure and development of this organ. Sections made longitudinally through young flower buds reveal a nearly sessile ovary usually containing two parietal ovules each, on a short funiculus (Plate LXXIX, Fig. 8). There are 11 to 13 bundles which extend through the base of the ovary to the tip, branching more or less in their course. Along the inner edge of each bundle are tannin pockets. After the egg is formed and fertilized, the reduced ovarian axis begins to elongate to form the gynophore. The ovary and embryo sac remain unchanged in this condition until the gynophore is mature. This will be further discussed under physiology. The later cytological study of the embryo was not attempted.

The meristematic tissue which gives rise to this growth is mostly situated just below, and around the base of the ovary. That below the ovary forms the pith, while that around the base forms the bundle tissue and outer cortex. A few dividing cells forming the latter were found well up around the ovarian cavity. The epidermis of the tip becomes sharp pointed and highly lignified in its outer walls. In Plate LXXIX, Fig. 9, is seen the area at one side of the tip where the style was formerly attached. This style is terminal in very young buds, but the later lateral position of the scar is prearranged for by a special development of a few large lignified epidermal cells at one side of its base. (Plate LXXIX, Fig. 8). These grow forward a little, and form the sharp point of the ovary.

Anatomy of the Mature Gynophore. While the structure of this fruit stalk corresponds to that of the stem of any herbaceous dicotyledon, its manner of development resembles that of ordinary roots. There are no lateral appendages, and so no nodes and internodes. There are two distinct divisions of this organ (1) the epigeal part, with smooth, red pigmented surface bearing a few three celled hairs similar to those on other parts of the plant; (2) the hypogeal white part, whose surface produces single-celled absorptive hairs. (Plate LXXIX, Fig. 7.) The surface of the aerial portion is covered with

stomata and lenticels. The epidermal layer of this has a few scattered crystal cells similar to those found on the stem.

The cortex is composed of six to eight layers of round thin walled cells. Internal to this is the vascular system composed of a ring of bundles, each with a large patch of highly lignified bast on its outer side.

Concerning the cambium layer, Pettit says, "There is an indication of the formation of a cambium ring, although it never occurs even in the oldest portion of the organ." She goes on to explain the apparent presence of meristematic tissue between the bundles, which the writer considers interfascicular cambium. She continues, "The cells are, in their early stages, no larger than the pith cells, but as they become older they increase rapidly in both tangential and radial diameters. This process, however, appears insufficient to keep pace with the growing intrafascicular cambium, and they now become meristematic, forming new walls which are at first tangential; later radial walls are found. In this manner arise clusters or bands of relatively small cells extending from bundle to bundle. While these small cells appear like the ordinary meristematic tissue of stems whose cambium is formed after the bundles appear, they do not continue meristematic; at least in the organs studied there is little evidence that these small cells produce lasting tissue of any kind, and none whatever of the formation of phloem and xylem elements." The above description is correct for the cause and manner in which they develop and appear, but the writer feels that this tissue is in all respects meristematic as a part of a continuous cambium ring. The author has seen xylem and phloem elements cut off from it to form secondary bundles, and thus proving that it has the ability to form these. Also, the presence of such cells in a nearly continuous line with the intrafascicular cambium suggests an hereditary tendency to form it even though it is less active than in other stems. It does apparently connect the xylem patches, but so does the corresponding tissue of many stems. The fact that they divide even once is sufficient proof, since the resulting cells are permanent. The pith is composed of thin walled cells stored with starch until the fruit begins to form. Later the pith breaks down as does that of the stem and the gynophore becomes more or less hollow.

The anatomy of the subterranean part of the gynophore differs from that above ground in the following ways: (1) All of the epidermal cells become extended outward into long absorptive hairs

simulating typical root hairs. (2) a growth in thickness occurs by a process similar to that of periderm formation, by which the diameter of the subterranean part is somewhat increased. Pettit notes another difference in the absence of what she calls *plasmolytic cells* situated in the center of the cortex of the epigeal part. These cells have not been observed by the author.

The absorptive hairs (Plate LXXIX, Fig. 7) are large, unbranched, one celled and average nearly a millimeter in length. Each is slightly enlarged at the base which represents the size of the original cell from which it springs. No stomata were seen, but lenticels were present which developed into a white proliferation of cells when exposed to a moist atmosphere as did some of those of the epigeal portion.

The examination of a cross section of this hypogeal area showed the outer layer of the cortex dividing into two to four layers of cork-like cells. The cells of this sub-epidermal layer are somewhat larger than those of the rest of the cortex. Although these apparent phellogen derived cells have tbe appearance of periderm, according to Pettit, they are free from suberin, as would be expected from the presence of absorption hairs on their exterior.

Anatomy of the Young Fruit. As noted above (see page 316) the ovary, situated at the tip of the gynophore remains inactive until the time comes for fruit maturation. The epidermis at this time is composed of much deeper and narrower cells radially, than that of the non-hairy part of the gynophore. They become deep, tapering and lignified at the tip forming a hard, but not capped apex. The lumen of those at the tip contain numerous granules that are not evident further back and suggest a relation to the geotropic reaction of the gynophore. Three or four hypodermal layers, that later form the outer mesocarp, are composed of markedly cylindric cells. A branching bundle system within this is a continuation of that of the gynophore which gradually disappears toward the tip. Just interior to this are a few layers which later assume marked appearance and importance as tissue which becomes gradually lignified to form the strengthening inner shell layer of the fruit. The innermost tissue next to the ovarian cavity is composed of several layers of tiny nearly square cells arranged in radiating rows.

Anatomy of the Developing Fruit. When the ovary begins to enlarge, the epidermal cells elongate longitudinally and later become ruptured. This epidermis with the subjacent layer, is rubbed or

stripped off, which is a very unique event in fruit maturation. Apparently the epidermis does not keep up with the growth from within. Within the epidermis several layers of periderm have already appeared, similar to, and continuous with, that of the lower end of the fruit stalk (gynophore). Till this occurs and until the fruit is one half to three quarters full size, no hairs are formed on any part of the ovary or young fruit. About this time, however, and lasting until the fruit is mature, there appear on this layer irregular, often branched, one-celled absorptive hairs (Plate LXXIX, Fig. 6).

The developing bundles have increased in size, and with their connecting branches, form ridges which later give the reticulations to the fruit. Meantime a few layers, just interior to these, are becoming remarkably indurated to constitute the solid enclosing chamber of the mature fruit. The inner endocarp area of small cells has enormously thickened and from the time the fruit has begun to swell until nearly ripe, this area is composed of very large, thin walled, pith-like cells which contain sugar. This area remains thick and the developing seed small until a short time before maturity. It forms a large part of the fruit at this time.

Anatomy of the Mature Fruit. Winton notes the presence of an epidermis and states that it is not easily seen. As noted in the discussion of the developing fruit, this could only be a pseudo-epidermis that he has mistaken for the already shed epidermis, and the fact that it is the small-celled third layer of the ovarian tissue may explain why it is distinguished with difficulty. As in the nearly mature fruit, absorbing hairs are present as wall extensions of it. These hairs were not observed to be as often branched as in the younger fruit. One or two appeared to be septate.

Just below the outer absorbing layer are several rows of brick shaped, thin walled cells, simulating those of the hypogeal gynophore in appearance and position. Within this are several layers of thin walled cells that have collapsed. Apparently new cells were not produced for this area to allow for the expansion of the fruit. These surrounded a few layers of unbroken, rounded cells in which are embedded the branching vascular bundles. Large bundles are arranged longitudinally, and are connected by short smaller cross bundles, the whole system forming the reticulation of the peanut shell. The xylem and phloem of these have become highly lignified.

Attached to the inner edge of the bundle network is the solid hard enclosing shell of the peanut, composed of the now mature lignified

mass of cells mentioned in connection with the maturing fruit. The cells forming this are now remarkable in their shape, size, wall thickenings, and branches. (See Winton's article.)

The structural relation of the carpellary wall to that of a leaf, from which it is modified, is recognized, but with more difficulty than that of many aerial leguminous fruits. By carefully splitting open a fruit, as one ordinarily shells a peanut, it will be noted that the seeds are attached to the somewhat convex side opposite that of the beak. Thus the dorsal is recognized from the ventral suture. Histologically these areas are not discernable in young ovaries, except by noting the location of the ovule attachment, or that of the style. This also locates exactly the position of the beak in the mature fruit. In mature fruit shells there is a ventral suture along which they quite readily split, due to a weaker, less lignified, loose line of tissue as seen under the microscope.

Concerning the exocarp, mesocarp and endocarp and their origin, there is such a marked change and fusion of parts that any sharp line of demarcation is impossible. The exocarp, which is typically derived from the lower leaf epidermis, is lost during fruit maturation. The name endocarp, derived from the lower epidermis, might be applied to the soft, internal tissue called inner parenchyma by Winton. Practically the whole of the shell then would be the mesocarp and can be subdivided into *hypoderm*, *bundle area* and *bre layer*.

The anatomy and cytology of the embryo not having been attempted, that of the mature seed is also omitted. For details oJ the latter the reader is referred to Winton's article.

Physiology

Root Hairs

To the writer, the thought suggested by others, as noted in the histological discussion, that *Arachis* bore no root hairs, seemed contrary to expectation. The plant, with a semi-xerophytic tendency, and growing well in a warm, loose soil, would be expected to have them, at least when moisture is sufficient to stimulate their production.

Plants started in the greenhouse and carried on in flower pots were therefore examined. Of twenty-five plants, one showed hairs present near the tips of two of the young vigorous growing roots.

They were, however, very short and comparatively few in number. It was noted, however, with some surprise, that on the roots of nearly every plant, tufts or whorls of hairs were present as rosettes at the base of some of the side rootlets. These were much longer than the first-mentioned type, as is set forth in the figure. The possibility that the influence of potting may have in some way caused the development of these rosettes as well as tip hairs, led to an examination of the roots in the center of pots, and of roots on plants which had been carried forward in boxes (2 x 3 x 1½ ft.) Such roots have less air drainage than those along the inside wall of a flower pot. Plants were removed, their roots carefully washed out, and tufts of hairs were found at the base of many newly formed side roots.

The presence of normally produced tip hairs was carefully watched for, but none was found. The only plant mentioned which had these was one, the roots of which were in a moist air compartment, formed by the drainage hole of the bottom of the flower pot, the broken crocks just above, and the cinder bench below. This suggests, therefore, that optimum oxygenation is a necessary factor for the tip hair growth. None were found on the roots of any plants in the soil, either under dry or moist conditions. Since the plant seemed to have at least a hereditary tendency under certain conditions to produce these normal tip hairs it was considered worth while to determine, if possible, the exact causes or stimuli which affect their growth and that of the rosette type. Observations and experiments were, therefore, carried on with this in view, as well as to determine the causes and method of production of, and differences between, the two forms. The results of this investigation are described in succession to the following discussion of the works of others on this subject.

Concerning the presence and absence of root hairs, Strasburger[20] states that in some few instances as in some conifers plants bear no root hairs. Jost[21] says that few plants produce none, probably referring to aquatic types. Haberlandt[22] refers to two stages in the specialization of absorptive tissue in plants. (1) Some plants are content to increase their absorptive surface by a greater output of side roots, the epidermal cells of which are flat or slightly convex in their outer walls. But he states that this type includes marsh and aquatic plants, and is less advanced in this regard. If this is a stage in specialization, would it not be possible to think of it as a reduc-

tion change following a former evolved condition in root hair production due to adaptation to changed environment? Corn and many other plants produce none when put in water. (2) Other plants produce root hairs near the tips of their roots by elongation of the outer epidermal cell walls. Since many hair producing plants cease to bear these when in contact with water or saturated soil, it would seem to the writer that instead of being two stages of specialization, it is an example of two types of absorptive tissue dependent on ecological factors. It is a more or less epidermal surface extension for absorption, dependent upon the amount of causing stimuli present. The hairless aquatic plants may have had hairs at some time, and some do produce them when growing in dry soil again.

As to the cause for root hair production, Pfeffer[23] states that too little or too much water hinders, while darkness and contact accelerate. Snow[24] in an extensive investigation on the causes of their development finds that they are accelerated by a retardation of growth, by mechanical means, or substratum resistance, especially if the roots of such are allowed to grow in a moist atmosphere. She finds that they are retarded by a saturated atmosphere at high temperatures, by a lack of oxygen, and by a saturated soil; light and darkness, however, have no material effect.

Observations and Experiments with Root Hairs

It was noted that if seeds were planted in a heavy soil and germination was retarded by lack of moisture, the hypocotyl would sometimes swell considerably and give off adventitious roots which branched profusely. By drawing the soil away, after the radicle had grown an inch or two, until the lower end of the hypocotyl was well exposed, the upper part of the side, and of the adventitious roots with their hairs could be kept growing in saturated air. This gave a good opportunity to determine the effect of sunlight on the growth of hairs, as compared with those on a few plants whose roots were kept in the dark, but also exposed to the air. The foliage of both sets of plants had the same leaf exposure, so that the activity and growth were as near the same in all as possible. In all cases, both in light and in darkness, the rosette hairs were found at the base of the side rootlets and there was no marked difference in their size or abundance. This corresponds to the results of Snow, except that in her observations she noted a slightly longer growth in the

dark. This was possibly due to a greater drying out in light in her experiments. No normally produced tip hairs were observed.

Temperature. Plants with roots exposed were kept at 90° F. to 100° F. in a moist chamber. Others were kept at 60° F. to 70° F., the other conditions being the same. Rosette hairs appeared on all the plants, but at the higher temperature they were much more luxuriant and abundant. Tip hairs were found near the tips of several roots on two of the plants growing at the high temperature. These two plants producing both types of hairs were the most vigorous of the set of twenty in the experiment. These results do not correspond with those of Snow, where a high temperature and humidity retarded their growth. This can possibly be explained by the fact that the peanut requires a higher temperature for optimum growth than those plants with which she experimented.

Soil. Plants in loose sandy soil composed of one-half light loam and one-half sand grew vigorously. After germination they produced numerous long and almost pure white roots, a few of which, after reaching the side of the pot or box, bore a limited number of tip hairs. No rosette hairs appeared until the plants were one to two weeks old and quite well established. Tip hairs appeared on one plant only, of those that were older than three weeks. Plants in light loam, without any mixture of sand, grew slowly and the rosette hairs were the first and only type observed, after the side roots had developed. They appeared on all the plants examined after from one to two weeks' growth. Tip hairs were observed on a two months' old plant which had been retarded in its growth, and, when repotted, a few delicate roots appeared which bore a very few scattered tip hairs.* Rosette hairs could be found on any plant of any age, except the young vigorous specimens of less than two or three weeks' growth.

On seedlings of various ages no hairs of either sort were ever observed on the primary root. Many seeds germinated in sandy soil, and on sterilized wet cotton in test tubes, did not produce them even under optimum conditions of heat, air and moisture. With sufficient moisture, however, rosettes always appeared on the bases of the side roots. Those in test tubes grew slowly because of lack of

*Of about fifteen such plants examined this one was the only one in which they were observed.

water, and as a result rosette hairs were the only type observed. These were absent on the roots furthest from the moist cotton.

Concerning the function of root hairs on the radicles of seedlings, Haberlandt and others state that one reason for their early formation on these, is, that the main root may have sufficient anchorage in order to rapidly penetrate the soil for its immediate needs. Evidence presented by the peanut thus entirely contradicts such a view, indicating that they are not necessary for this purpose. Such seeds as those of the peanut can alone supply adequate food material for germination if water is present. The radicle elongates and penetrates a light soil with great rapidity without them. This may be one reason why a light sandy soil is best for this species. This thought also suggests an interesting relation to the hypogeal fruit production. The plant always maturing its seed under ground would not need such anchorage for its first root growth, even though it were a desirable feature. The fruit wall acts also as an aid. The writer feels, however, that the reason why hairs are not present here is that the outer layers, in stripping off (see page 314), do not allow their development. The fact that side roots, which do not show this peeling, will form them under proper stimuli is evidence of this. Even these do not often produce them, probably because of their very loose structure (see page 314). The cells which are best adapted to respond are at the base of side roots, thus rosettes are formed.

To summarize these observations, the results of the root hair experiments on the peanut indicate that (1) light and darkness have no effect on their production; (2) high temperature, with sufficient moisture and air, accelerate the growth and production of the rosette type; (3) loose sandy soil, with root aeration, stimulates hair growth on the tips of young plants, and possibly also on old plants, if a period of retardation is followed by a suddenly renewed root vigor. The rosettes of hairs may appear on any plant of more than one to two weeks' growth. The tip hairs are found only on young roots that are undergoing a vigorous elongation in a natural or artificial moist air space at a high temperature. Low temperature, lack of oxygen and wet heavy soil prevent the normal tip type from appearing and retard the rosette form. None appear on the radicle. The cause for the production of the rosette hairs at and on the base of the side roots is hard to explain. It may be that, at the time the side root is penetrating the cortex and epidermis of the main root,

the root tip tissue here is more active and vitalized than later, and so is more sensitive to external stimuli. It was noted that when tip hairs were produced usually no rosettes were present. Possibly these offset the need for tip hairs, or at least utilize energy which is lacking for their later formation.

Absorption

From the foregong observations on the roots and root hairs of the peanut, it is evident that the young plant absorbs its water and mineral foods by any one, two, or all of the following means, depending on environment and growth conditions: (1) Through the epidermis of young roots the thin cuticle of which is mucilaginized; (2) By means of normal tip hairs on vigorous growing roots; (3) By means of the rosetted, basal hairs. The first and last are undoubtedly the most important of these. As soon as the fruit stalks appear and reach the soil, hairs are at once formed from the epidermal cells of these. The older plants then have a much more extensive absorbing surface from the formation of a considerable number of gynophores.

Proof that these hairs do supply water to the plant is indicated by the fact that, according to Pettit, when the roots of such are severed the plant continues active and apparently uninjured for some time. The xylem of the gynophore bundles, although not very large, is sufficient to carry a considerable quantity of material. The nearly mature fruit must also absorb some water as indicated by the presence of delicate absorbing hairs. How important this is it is difficult to say. That they are not absolutely essential is evident from the fact that the fruit continues to swell somewhat if transferred from the soil to the air, causing the hairs to dry up. The absorbing fruit stalk undoubtedly takes the place of roots to a certain extent. Root tubercles, which also appear at about the same time, should be noted too in this relation, since some other nodule-producing members of the Leguminosae, as is well known, seem to have a reduction of root hairs. The absorbing surface of roots alone on these older plants is comparatively small.

Development

Germination. The writer, in attempting to raise plants for study in the greenhouse, had some difficulty in keeping insects and mice away. Some of these seemed to have no difficulty in locating the seed even before germination. A wire cage was finally built which

controlled these pests. Further trouble was experienced, however, unless great care was used in planting and watering. It was found that unless they were brought forward in loose material like sphagnum or well aerated sandy soil, they rotted in one to two days. If pure sand were used, they would rot if kept even moderately wet. The method finally used which succeeded was to plant several together, allowing a considerable degree of aeration. When these produced an inch or two of radicle, they were separated and transferred to individual pots with the cotyledons half exposed. Seeds planted in the shell succeeded well, as this seemed to allow also for free aeration. The ease with which the seeds rot is likely due to its weak protection by the testa. This thin papery coat is easily ruptured and the embryo, rich in food material, seems to be very susceptible to infection by molds and decay-bacteria. If growth is rapid, however, the increased oxidation gives it vitality to resist. Those who raise peanuts say that good drainage in a loose soil is absolutely essential for success. The plant must start quickly and be kept growing. If planted in the uninjured shell, which is sterile within, there is less likelihood of infection before it gets well under way. A comparison was made by Bennett[25] of growing peanuts from shelled nuts, nuts broken into two parts, dry and unshelled nuts, and unshelled nuts which had been soaked in water for 12 hours and buried in the earth below the frost line for different periods. The most perfect stand was obtained from nuts planted in broken pods. The results seemed to indicate that when nuts had been thoroughly wet and moist for a short time they would produce a good stand, and save the expense of shelling. This corroborates the author's thought that the seed benefits by free oxygen and protection furnished by the shell in order to start its growth successfully, at least in anything but an extremely loose soil.

Later Growth. After the radicle has reached two or three inches the cotyledons are pushed about 2 cm. into the air by the elongating hypocotyl. The hypocotyl often becomes thick and fleshy in its cortex. This is more marked when growth is retarded from some cause, and then the lower end becomes tuberous from a deposition of sugar. The roots of such are not able to utilize the food as fast as it is supplied from the seed. When the soil is light and the temperature optimum, the formation of an extensive root system results (see page 323). Under these conditions while the food of the cotyledons is still available, the plant grows rapidly for about

two weeks, followed by a period of very moderate development. Audouard[26] states that the plant grows slowly during the first half of its existence, and that the most rapid growth takes place after about ten weeks. This indicates a relation to the formation of the gynophore and root tubercles again, both of which appear later. This makes possible a greater activity in growth of the plant. One feature somewhat difficult to understand is the presence of the numerous stomata on both epidermal layers. How is the water balance kept with such a reduced hair surface, especially on the roots of plants not yet producing fruit?

If the seed is deep, the hypocotyl elongates accordingly. If the seed is planted in the shell, it will push up through three or four inches of soil. It is often much curved and twisted in its efforts to extricate the cotyledons from the shell. These remain green for two or three weeks, when they wither and drop. Concerning the presence of food materials during growth Audouard states (1) that there is sugar in all parts of the plant, which decreases in amount during fruit maturation; (2) That starch in the root and stem increases from the beginning to the end of vegetation; (3) that fats increase for six to nine weeks, that is, until the fruiting period, when they suddenly decrease in the vegetative organs; (4) that proteins decrease in roots and stems at flowering time and increase in the fruit. The writer has observed that the gynophore is well stored with starch until the ovary begins to grow, when apparently much of it is carried as sugar to the inner fruit tissue, forming there the broad, delicate-walled sugary endocarp (see page 319),—thus the reason why immature fruits are sweeter. Some of this sugar at least is apparently gradually transferred to the testa and there stored temporarily as starch. Later, both this and that from other sources (gynophore and stem) are transferred to the cotyledons and largely stored as oil. Since the carbohydrates are early furnished and carried to the gynophore and stem, the thought arises as to the possibility of the fruit maturation being largely independent of the roots of the plant. The other food materials can be obtained from the soil by the fruit, and proteins can be formed in darkness, so there is no known reason why this should not occur.

Biological Considerations Concerning the Fruit and Gynophore.

Observations on the Gynophore. In his work on "The Movements of Plants," Darwin[27] says that while apheliotropism may act in

some slight measure on the downward growth of this organ, geotropism is unquestionably the exciting cause. The writer proved this by inverting two plants which had produced several gynophores whose tips were about to pierce the soil. As seen in Fig. 11 the tips turned away and became reversed in position. This not only proved the effect of gravity, but also that the hydrotropic reaction of the organ was weak or lacking. They acted in a similar way even if the soil was saturated. When tips were allowed to penetrate wet sphagnum, and then the plants reversed, they would recurve downward and grow out of it. When the plants were righted again the tips also turned back thus forming an S curve (Plate LXXX, Figs. 11 and 12). The presence of definite granules in the lumen of each of the epidermal cells of the gynophore (see page 318) at the tip, and their absence anywhere else, suggests the possibility of such being the structures by which this organ perceives when it is out of line with gravity. This has been discussed by others in connection with the presence of starch grains in root tips. The writer found that by cutting off the tip of the gynophore, growth continued, but there was no reaction to gravity when the plant was inverted. The apparent homology between the behavior of the root apex and of the gynophore apex is highly suggestive.

Darwin refers to the means by which this organ penetrates through the soil. He says, "the sharp smooth point of the gynophore enables it to penetrate the ground by mere force of growth, but its action is aided by a circumnutating movement." The anatomy of the organ is also suggestive. The patches of hard bast give strength, while their separation, even though in a close ring, gives pliability. Pettit states that the hairs produced at the tip are also an aid in holding it firmly. Although this happens to be of some assistance, the writer would question to what extent, since the relation of the radicle to soil penetration puts a new light on this matter. Hair experiments, similar to those of Pettit, were made with plants bearing young gynophores, which had not yet reached the soil. Pettit found that by putting these in a moist chamber a narrow zone, averaging 3 mm. in length, always appears one to eight millimeters from the tip. The writer found by repeated experiments that this zone might be as much as 5 cm in length (Plate LXXX, Fig. 13).

In discussing these in relation to those of roots, Pettit says: "In comparing the growth of gynophore hairs with that of root hairs it must be remembered that the growing point of the gynophore cor-

responding to the punctum vegetationis of the root lies just below the ovary which occupies the extreme tip of this organ. The ovary, however, is almost microscopically small and remains so during the growth of the gynophore. To illustrate the extremely small space occupied by it, the hairs which were not more than one millimeter from the tips of the gynophores as mentioned above were still below the growing point under the ovary. While this difference in the position of the growing point exists between root and gynophore, the difference which it makes in estimating the relative distances of the hairs from the tips is practically nothing.

"The resemblance between these hairs and those of roots was further tested by repeated experiments in pulling young gynophores carefully from the soil. The minute portions of earth clung to the hairs and refused to be separated from them in the same manner as in the case of root hairs. In several instances these hairs were tested for acids and were found to respond readily to the litmus paper test.

"Still another experiment was made which furnishes strong evidence that one function of the gynophore hairs corresponds to the chief function of those of the root. A large, well developed, thriftily growing plant was cut in such a manner as to separate the whole root system from the stems, but the latter were still connected with the ground by numerous well grown gynophores. The result was that the plant so treated after two weeks still presented nothing to a superficial inspection to distinguish it from others in its vicinity whose roots were left intact. Closer examination showed that some branches were dead; but the majority were putting out new leaves which appeared quite as strong and healthy as any of those on similar plants in the vicinity which were supported by roots. Unfortunately these experiments were begun late in the season, and the appearance of the frost prevented their continuance."

Fruit Maturation. Other writers state that all attempts to make the gynophore produce aerial fruits by digging away the soil as the gynophore elongates fail. It is also well known that any such stem dries up unless it reaches the soil by the time it is two to three inches long. The length to which it grows before drying varies with the humidity of the air. Experiments were thus made in an attempt to determine what caused the ovary to enlarge, and what would prevent it. Plants with gynophores of various lengths were put in a saturated atmosphere and not allowed to penetrate any substratum. In all cases the gynophores continued to elongate and become green

for about a month. They usually attained five or six inches in length and then wilted just back of the ovary. The longest gynophore produced in this way was seven and one half inches in length —nearly twice as long as any seen by the writer in the soil. Hairs developed which gradually died away until there were but a few near the tip. Other gynophores were allowed to grow in test tubes of tap water, some kept in the dark, others in the light. These produced no hairs. Two of those in darkness, after eight weeks, produced a small one seeded fruit. The remainder produced none. Others were allowed to grow into sphagnum and pure sand and resulted in fruit formation in both cases. Gynophores which had penetrated soil and whose ovary had begun to swell were exposed to a saturated atmosphere and to ordinary greenhouse conditions. In the former case, the fruit turned green and continued to grow slightly, while the latter turned green and remained small.

The results of these trials, although not at all conclusive as to evidence offered, indicate that (1) a *thigmotropic*, *hydrotropic* or *apoheliotropic* stimulus, or a combination of these, is necessary for the ovary to begin maturation, but (2) that a continuation of such is not necessary, since the ovary continues to develop somewhat if removed from the soil after its growth has begun. This development, however, is somewhat abnormal. All successful experiments were produced in complete or partial darkness, although those in the moist dark chambers failed. This suggests the necessity of the first two factors, i. e., water and contact. More research is necessary in order to clinch this point and determine which of the three is the most important.

From the writer's observations and from the varying results of the above attempts at fruit production, he feels that two things should be kept in mind—(1) the condition and activity of plant growth, (2) the ability of the plant to possibly supply the necessary substances to the fruit in two ways—(a) by direct absorption of some of them from the soil with the carbohydrate supply from the plant; (b) by transfer of all necessary materials from the vegetative organs into the fruit. A number of plants that became pot-bound, when several gynophores were being formed on them produced only one or two small fruits. Similar plants that had abundant potroom produced several. Weak plants may have been experimented with. In the field, many poor fruits without seeds called "pops" are found—due possibly in part to this same cause.

The chlorophyll formed in the fruits exposed to light was found to be exterior to and around the bundles that form the pericarp reticulations. The testa and cotyledons also became green. This is an interesting point since it indicates the retention through long millenia of the factors necessary for chlorophyll formation.

Watt has observed in India that red ants are frequently found working harmlessly around growing fruits in the soil. This would be of benefit to the fruit since aeration of the surrounding soil would allow for greater absorptive hair development. What benefit the ants might obtain is hard to tell.

Fruit Hairs. It should be kept in mind that the fruit hairs are different in origin from any found elsewhere on the plant (see page 319). Points of evidence indicating this are—(1) that the epidermal and subjacent layer of cells is seen to be thrown off (see page 319 and Fig. 6). (2) That the hairs are different from any found elsewhere on the plant, all of which are truly epidermal. (3) That this difference, that is the bifurcations of the hairs, indicates the irregularity of growth of the mesophyll of leaves. (4) That no hairs appear on the fruit until it is well grown and the two outer layers have been discarded.

Other queries raised here are: why is the second layer of cells discarded as well as the epidermis? and why doesn't the periderm-like tissue begin its formation by divisions taking place in this layer, as is the case with the hypogeal gynophore, instead of in a deeper layer? One possible answer is, that this corresponds to that layer of water storage cells next to the lower epidermis of the leaves of *Arachis*. This layer still persists in the carpel, and, being large-celled and less able to divide, is thrown off with the epidermis.

Conclusions from Physiological Studies

It remains to be considered how far the facts ascertained in this study contribute to the knowledge of hypogeal fruit production. The fact that the fruit of so many plants of varied families seeks the ground must be regarded as significant. Tschirch,[28] in a paper on Leguminosae, says that one group of nitrogenous compounds produced by the Leguminosae can be formed only in darkness, and suggests this reason for such a habit. It has also been suggested that the fruit is thus protected from animals.

Concerning the present studies, the following new facts stand out quite prominently—(1) The tendency to fruit formation in

moisture and darkness. (2) The formation of periderm-like tissue on the hypogeal gynophore and fruit. (3) The formation of hairs on the gynophore-epidermis and pseudoepidermis of the fruit. That water is absorbed by these hairs is undoubtedly true. The most puzzling new structural feature is the second, where thin-walled cells, not suberized, are laid down by a late-formed cambium layer. Such is rare in leaf tissue. The bud scales of Horse Chestnut and other trees produce a limited amount of suberized tissue in this way. Two to three layers are always produced on the gynophore when this organ is subjected to a saturated atmosphere. This suggests a possible water storage tissue, or it may be a result of pressure from within when more water is absorbed. Cells are possibly necessarily cut off to allow for this expansion.

Finally, it is suggested that if the plant does not require more nourishment from the soil than might be supplied by root hairs, and yet forms such hairs on the gynophore and nearly mature fruit, it may be more advantageous to take some of its food by this special method. Perhaps certain desirable changes are made possible by such foods always being in darkness. Is it then darkness, or extra water supply that the fruit seeks? Whatever the reason, the resulting advantage is full maturation and selective survival of the seed, which is highly concentrated in its food constituents.

Uses of the Peanut

To most people outside the peanut growing sections of the country, the peanut suggests only an unessential food article,—a delicacy to many,—in the form of the roasted or salted nut, peanut confectionery or peanut butter. During recent years, however, and especially in the past year or two it has become of utmost importance as a staple article of diet and otherwise. In the cotton growing states it is saving the day for many farmers who have failed with cotton growing because of the new insect pests or other reasons.

Uses as Human Food. The following from Beattie[29] in this connection is worth quoting: "The use of the peanut for eating from the shell is most important and popular, but the quantity of shelled peas that are first roasted and salted and sold by the pound is constantly increasing. Some of the better grades are first shelled, then roasted after which the halves are broken apart and the germ removed giving the meats a blanched appearance rendering them very desirable for table use. Great quantities of shelled peas are used

every year in the manufacture of peanut candies and brittle, both alone and in combination with other nuts, pop corn or puffed rice."

During recent years great quantities of shelled peanuts, especially of the Spanish variety, have been employed for the manufacture of peanut butter. It is used in the preparation of vegetarian meats after a portion of the oil has been pressed from the nuts. This extra oil and that pressed from nuts grown for the purpose is used in thinning peanut butter and is as good for every purpose as is that of the olive. It is one of the sweetest vegetable oils. Articles fried in it keep well for a longer time than in olive oil and have an agreeable odor and flavor. It is mixed with cotton-seed oil to improve it for salad purposes.

Peanut meal or flour of finely ground nuts is used in confections, cakes and bread making. It is used as a substitute for rice and other flours. Watt reports that in India the unripe nuts are sweeter (as indicated in the author's discussion on the physiology of the fruit) and, being more easily digested, are given women whose milk supply is insufficient for their children. These unripe fruits, when fresh, make an agreeable boiled dish. The very tender leaves of the plant are sometimes cooked with ground coconut.

Concerning the food value and change of the peanut from the category of a luxury to that of a more staple item of diet for man, the following is taken from "The Literary Digest" for April 13, 1918. "The peanut enters into the preparation of most of the vegetable 'meat substitutes' long warmly advocated by the vegetarians and now made more conspicuous by the governmental admonition to 'eat less meat;' and peanut 'butters' or 'pastes' are widely used. To-day the value of the peanut crop, which is divided between the production of the promising peanut-oil, peanut-cake for animal fodder and roasted peanuts for human food, has begun to total many millions of dollars. At the University of Wisconsin, Daniels and Loughlin have demonstrated by feeding-experiments on animals that the peanut can supply adequate protein . . . in sufficient proportions for growth and reproduction. It can also furnish an abundance of the water-soluble vitamin. The food as used in the human dietary does not, however, yield the growth-promoting fat-soluble vitamin, which has come to be recognized as a remarkable constituent of butter fat and egg fat; nor are the inorganic constituents adequate in quality to supply sufficient calcium and certain elements. Of course, the peanut is not used as a sole source of nutrients for

man; nevertheless, the delineation of its physiologic value enables one to define more intelligently the place which it can take in the ration. Daniels and Loughlin foresee an increasing usefulness for the peanut, now that its real value has been scientifically established. When we consider the broad areas, they say, which may be adapted for growing the crop, and the fact that our food supply tends toward a wider use of the seeds of plants, it seems appropriate to expect that the peanut, when rightly supplemented, will form a staple article of the human dietary. Like the soy-bean, which has lately come into prominence in American homes, the peanut needs only to have added suitable inorganic salts and the fat-soluble accessory to make it a complete food."

Uses as Food for Live-Stock. Beattie is quoted in this connection as follows: "In the factories where peanuts are cleaned, shelled, and graded for the market there is always a certain percentage of cleanings and inferior stock that can readily be turned into stock foods. The outside shell, or hull, of the peanut, is rich in food materials, but is extremely difficult to reduce to a condition in which it can be fed. In large cleaning factories the shells are generally used as fuel, and the ash resulting therefrom is valuable as a fertilizer. often containing as high as 3 per cent of phosphoric acid, 9 per cent of potash and 6 per cent of lime.

"The thin brown covering of the peas has a feeding value almost equal to that of wheat bran. These hulls are especially desirable for mixing with the smaller particles of broken peas for stock feeding. In large factories where peanuts are prepared for the manufacture of peanut butter and similar preparations the waste in the form of small particles of the meats and the germs is considerable and this is sold to farmers for feeding purposes. In some cases the waste is mixed with a portion of the hulls and finely ground or chopped before leaving the factory. Peanut hulls make an excellent bedding for use in stables, and by using them in this manner and hauling the manure upon the land their full value can be obtained.

"Broken peas and germs are used largely as a food for hogs, but both should be fed in moderation and in combination with some grain, as the peanut fed by itself will produce a hog having soft fat and inferior meat. The famous Smithfield hams and bacon come from hogs that are fed partly on peanuts, the practice being to turn the hogs into the peanut fields after the crop has been gathered and allow them to glean the pods that were lost in harvesting. The

principal objection to the use of peanut by-products as stock feed is their tendency to become rancid very quickly. The germs, which are high in nitrogen content, become rancid and bitter in a short while and should not be kept on hand for a greater period than fifty or sixty days."

Peanut cake is a stock feed composed of the remains of seeds when expressed for oil and is extremely rich. As hay, peanut tops are worth just as much as alfalfa, pound for pound. Even the entire plant is used, and often chopped fine for this purpose. It forms a well balanced ration for dairy cows.

Use as a Soil Renovator. Here again the peanut is rapidly becoming a crop of much importance. Peanuts are valuable as a substitute for cowpeas, especially in certain soils that are not adapted to the growing of the cowpea. In many sections where the clovers and other soil-renovating crops will not withstand the heat and drought of the summer months the peanut will thrive and make an excellent growth. A crop of peanuts for forage can often be grown after the removal of oats or some other spring crop, and although they may be badly overgrown by crab-grass, the tops may be mown with the grass for hay, and the hogs turned in to root out the peas.

Miscellaneous Uses. The oil, beside its use as a food, is valuable in soap making, in lubrication and for illumination in some countries. The shell is often ground into a fine powder for polishing tin plate. It is said that tin plate manufacturers cannot get enough since this and middlings are the only two things that will put that mirror-like polish on tinware and not leave a scratch on the surface.

Summary of Results

The results of these investigations concerning the histology and physiology of *Arachis* present marked features which are summarized as follows:

1. It was found that root hairs were present on the plant, although reported as absent by two previous workers. These were usually arranged in rosettes at and on the base of side roots. Their growth is stimulated by a high temperature and humidity. The normally produced tip hairs appeared on very young plants whose roots grew rapidly and were exposed to moist air conditions. Later they never formed unless the plant showed a sudden renewal of growth vigor. Saturated and heavy soil conditions retarded the growth of the rosette type and inhibited the appearance of the tip hairs.

2. The hypocotyl shows a tendency to enlarge and become tuberous unless growth conditions are ideal. This is apparently due to a deposition of sugar from the stored food of the cotyledon which is unable to be cared for by the root as fast as it is supplied.

3. The stem is quite normal. Its epidermis, however, has crystal cells in groups of two to four. The pith breaks down causing the stem to become more or less hollow.

4. The leaf, with numerous stomata on both the upper and lower surfaces, has also, in both epidermal layers, small cells with a single contained crystal in each when young. Later these cells become fused into an "epidermal vessel," containing two to thirty crystals arranged in irregular rows or groups.

5. The fruit stalks or gynophores have been shown to be geotropic in reaction, and the epidermal cells of the carpellary tips are markedly granular, suggesting a possible perceptive relation in this regard. These organs are very weakly hydrotropic and do not react to light or darkness. The epidermis of the epigeal portion has crystal cells like those of the stem. The epidermis of the hypogeal part becomes elongated in the cell walls to form absorptive hairs. The second layer becomes cambioid forming a phellogen-like hypodermis, and this, by cambioid activity, may divide into two or three layers. The bundles are separate and highly lignified in the outer phloem and in the xylem. This gives mechanical strength for soil penetration.

6. The young fruit, as it begins to swell, bursts the epidermal and subjacent layers of the ovary, throwing them off. The next or third layer, now the pseudo-epidermis, forms irregular, more or less branching absorptive pseudo-hairs. These are different in nature from any of the other hairs formed on the plant, and are indicative of the irregular growth of the spongy mesophyll of leaves. Beneath this layer are developed several zones of cells similar to, and continuous with, the pseudo-periderm of the gynophore. This is a marked peculiarity in leaf tissue formation.

7. Attempts to produce peanuts in the air by various means failed to give definite results. Two succeeded by allowing the gynophore to grow into water; several when grown on sphagnum and also pure sand. None succeeded where the ovary was exposed to light. The results indicate that water is an important factor, but that contact, or darkness, or both may also be necessary. Young fruits, if previously in contact with soil, and then exposed to the air, continued to develop to a certain extent and turned green. The

re-formation and presence of chlorophyll in these indicate the retention through long periods of time, of factors for its formation in such a leaf structure.

8. The possible benefits derived from underground fruit formation may be (a) protection from grazing animals, (b) formation of certain proteins possible only in darkness, (c) more rapid and greater development in fruit size and number.

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EXPLANATION OF PLATES

Plate LXXIX.

Fig. 4. Root hairs (rosette type) as they appear on and at the base of side roots.

Fig. 5. A portion of the upper epidermis of a leaf showing numerous stomata and crystals in "epidermal vessels."

Fig. 6. A section through the outer layers of a peanut fruit which was about three-fourths grown.
- a—A portion of the epidermis and subjacent layer of the ovary still adhering.
- b—More or less branched fruit hairs developing from the former ovarian third layer, now exposed.
- c—Hypodermal tissue.

Fig. 7. A section through the outer layers of the hypogeal part of a mature gynophore showing:
- a—Hairs formed from the epidermal layers.
- b—Two layers of the periderm-like tissue (hypoderm).

Fig. 8. A longitudinal section through a young ovary just before the blossoming.
- a—Base of style.
- b—Pollen chamber.
- c—Enlarged and indurated cells which become the apex in Fig. 9.
- d—Ovules in ovarian cavity.
- e—Fibro-vascular bundles.

Fig. 9. A longitudinal section through a gynophore tip, the ovary of which is three weeks older than that of Fig. 5, and drawn to the same scale. Note the very slight difference in size, the style scar at *a* now pushed to one side by the enlarged epidermal tip cells which are shown at *c* in Fig. 8.

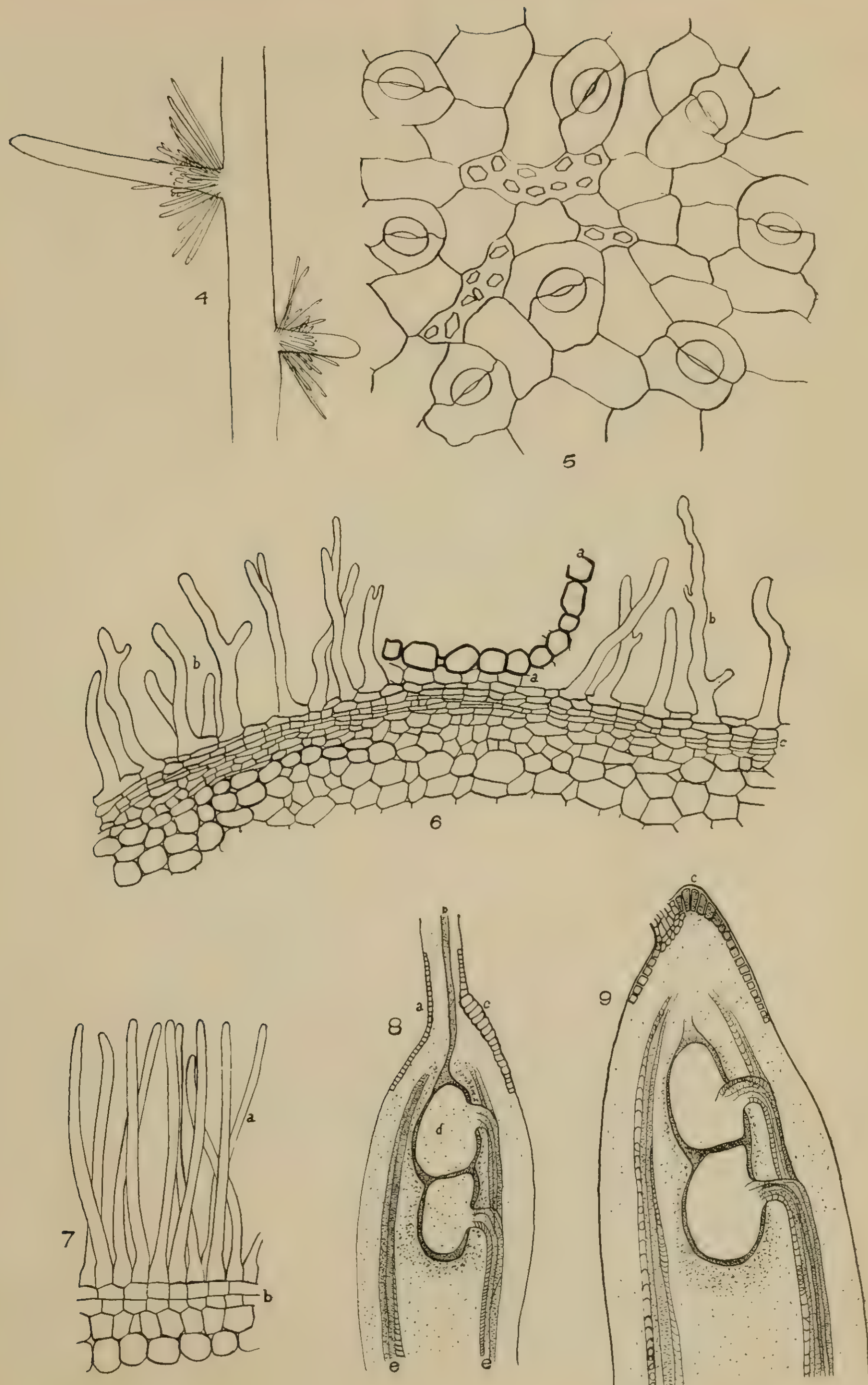
Plate LXXX.

Fig. 10. Photo of a Spanish variety peanut plant showing flowers, flower buds and gynophores clustered together at its base as is typical of the *fastigiata* subspecies.

Fig. 11. Photo of an inverted plant showing gynophores recurving in reaction to gravity.

Fig. 12. Photo of plant which was righted again, shown in Fig. 11. Note the change of the gynophore tips again.

Fig. 13. Photo of a plant which, after forming gynophores, was put into a moist chamber. Note the profuse development of hairs resulting.



WALDRON ON PEANUT

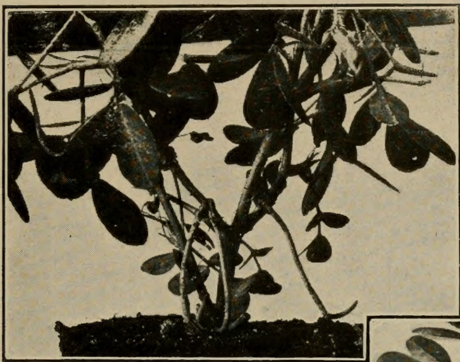


Fig. 11

Fig. 12

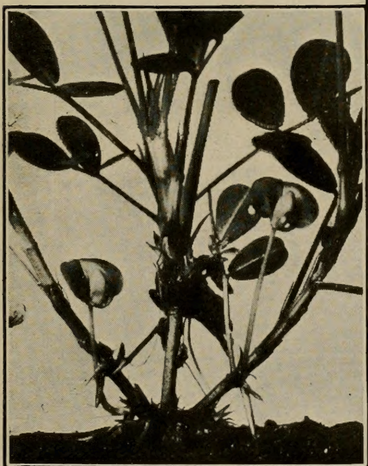


Fig. 10

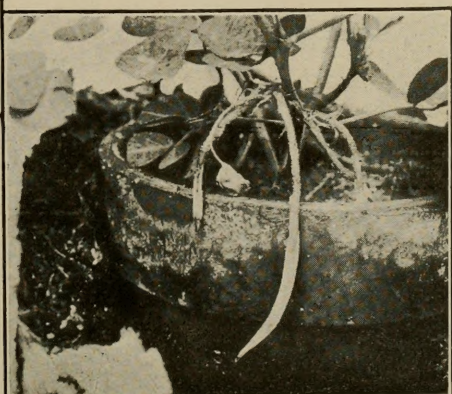


Fig. 13

WALDRON ON PEANUT